

Mark–recapture estimates of recruitment, survivorship and population growth rate for the screwworm fly, *Cochliomyia hominivorax*

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Abstract. Pradel model mark–release–recapture estimates of survivorship, ϕ , recruitment, f , and the rate of density-independent population growth, λ , are presented for eight mark–recapture studies of the screwworm *Cochliomyia hominivorax* (Coquerel) (Diptera: Calliphoridae) from Costa Rica, totalling 19 573 released and 4476 recaptured flies. Corroborative estimates of survivorship and the rate of population growth based on an extensive review of the literature are also reported. Weighted-mean \pm standard error of the mean (SEM) mark–release–recapture estimates of survivorship, recruitment and the rate of population growth were $\phi = 0.798 \pm 0.008$, $f = 0.193 \pm 0.008$ and $\lambda = 1.005 \pm 0.002$, respectively. Population doubling time was estimated from λ at 139 days. Estimates of ϕ and λ from the literature both exceeded those calculated by mark–recapture methods and estimates of population doubling times were consequently shorter.

Key words. *Cochliomyia hominivorax*, Calliphoridae, Diptera, Insecta, MARK, mark–recapture, Pradel, screwworm.

Introduction

The New World screwworm (NWS), *Cochliomyia hominivorax*, is a myiasitic fly injurious to livestock and human health (Steelman, 1976; Spradbery, 1993; Powers *et al.*, 1996; Wyss, 2000). *Cochliomyia hominivorax* was eradicated from the U.S.A., Mexico, Central America, Curacao, Puerto Rico and the U.S. Virgin Islands by the U.S. Department of Agriculture, Animal Plant Health Inspection Service, Screwworm Eradication Program, by an integrated approach, incorporating the release of sterile insects (Wyss, 2000). An eradication programme is currently underway in Jamaica, but the screwworm remains extant in the rest of the Caribbean and in South America.

Per capita adult rates of recruitment and survivorship, and the rate of density-independent population growth (hereafter f , ϕ and λ , respectively), are key life history parameters required for predicting population dynamics, for modelling the efficacy of sterile insect technique (SIT) control programmes and for estimating the rate of spread of potential new outbreaks. New World screwworm mortality rates have been estimated in the labora-

tory (e.g. Crystal, 1967a, 1967b; DeVane & Garcia, 1975) and death rates can be inferred from the results of some outdoor cage (Davis & Camino, 1968) and field (Thomas & Chen, 1990) studies. Recruitment rates can be calculated from laboratory estimates of life history parameters (references included in the Appendix). However, to date, no field estimates of NWS recruitment or population growth rates have been published.

Wildlife biologists commonly measure life history parameters for field populations by mark–release–recapture techniques (Jolly, 1965; Seber, 1965, 2002; Pradel, 1996), in which animals are sequentially captured, marked and released and recaptured. Survivorship, recruitment and population growth rates can then be estimated from the rates of addition and loss to the marked population through time. Increasingly, these methods are used by entomologists to estimate life history parameters as well (Anholt *et al.*, 1978; Stoks, 2001; Schtickzelle *et al.*, 2003; Joyce *et al.*, 2004; Nowicki *et al.*, 2005). This paper reports f , ϕ and λ estimates calculated by the Pradel method (Pradel, 1996) for eight fertile NWS mark–release–recapture studies carried out at two locations in Costa Rica. A total of 19 573 flies were captured,

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marked and released and 4476 were recaptured (datasets are described in detail in Materials and methods) in the eight surveys. The current study also investigates whether f , ϕ and λ varied among tropical premontane wet forest and tropical dry forest life zones, the wet and dry seasons, or male and female flies. Next, corroborative ϕ and λ estimates from an extensive review of the literature on NWS life history parameters are presented. Finally, calculation of doubling times was carried out for NWS outbreak populations under density-independent growth conditions from both mark–recapture and published parameter estimates.

Materials and methods

Datasets

In each of the eight mark–release–recapture studies, flies of both sexes were captured manually in sweep nets at four to seven observation stations baited with one of three attractants: (a) rotting beef liver allowed to age at ambient temperature for approximately 1 week; (b) Merino sheep infested with NWS or (c) Swormlure IV (SWL IV), a synthetic, volatile, liquid screw-worm attractant (Mackley & Brown, 1984) deployed in a 150-mL bottle with a cotton dental wick refilled at weekly intervals following the methods of Broce (1980). Flies were then marked by gluing numbered plastic bee tags (Chr. Graze KG, Weinstadt, Germany) to the scutum, released and then recaptured at one of the observation sites (potentially including the site of initial capture and release). Table 1 gives the: (a) location of each study; (b) mean latitude and longitude of observation sites; (c) dates of sampling; (d) the Holdridge life zone (Holdridge, 1947, 1967; Holdridge *et al.*, 1971); (e) season (wet or dry); (f) attractants used at observation stations; (g and h) total numbers of flies of each sex marked and released, and recaptured, respectively, and (i) publications providing additional details on methods.

Seven of the eight datasets were previously analysed by Matlock *et al.* (1993). Dates in Table 1 disagree with those in Table 1 of Matlock *et al.* (1993). Here, we report the dates of the first and last days of observations analysed, which represents a more accurate accounting than that presented in the earlier paper. The numbers of flies released in Table 1 differed slightly from those reported in Table 1 of Matlock *et al.* (1993). A small number of flies were reported as both males and females during their mark–recapture history. These flies were included in the analysis by Matlock *et al.* (1993), but have been omitted from the current analysis. The numbers of flies recaptured in Table 1 also differ from those reported in Matlock *et al.* (1993). Recaptures made on the same day as the initial capture, mark and release were counted by Matlock *et al.* (1993), but eliminated from the current analysis because parameters were estimated on a 1-day timescale (see below). In addition, the reduction in the number of flies released in the current study caused a concomitant reduction in the number of recaptures.

Statistical analyses

Mark–release–recapture analyses were conducted with the public domain software Program MARK (White & Burnham,

1999) available at <http://www.warnercnr.colostate.edu/~gwhite/mark/mark.htm>. Remaining statistical analyses were conducted in SAS Version 9.1 (SAS Institute Inc., Cary, NC, U.S.A.). For each study, estimates of daily recruitment f , survivorship ϕ , population growth rate λ , and the daily *per capita* probability of recapture of marked flies, p , were calculated by fitting the Pradel mark–release–recapture model to data (Pradel, 1996). All parameters were estimated for a 1-day timescale. The Pradel model defines recruitment rate, f , as the number of new individuals added to the population, per individual, per day and population growth rate, λ , as the ratio $\lambda = N_{t+1}/N_t$ where N_t and N_{t+1} are the population sizes at days t and $t+1$, respectively. Parameters were fit separately for males and females and were assumed to be constant (time and age invariant) within each dataset, but to vary among datasets. The Pradel model cannot fit age-specific survival rates (Pradel, 1996; Franklin, 2001). Although evidence from laboratory studies suggests that survivorship may be age-specific (Spates & Hightower, 1967, 1970; Davis & Camino, 1968; Milward de Azevedo *et al.*, 1992), survivorship can be closely approximated by constant survival rates. Furthermore, field estimates for Studies 1–3 (Parker & Welch, 1992 [Fig. 7]; Parker *et al.*, 1993 [Fig. 8]) are consistent with constant survivorship. Thus, Pradel estimates assuming age-independence of ϕ should be approximately valid. Recapture rates and the sex ratios of flies captured vary among attractants (Parker & Welch 1991a, 1991b). Two attractants were used simultaneously in four of the eight mark–recapture studies analysed (Table 1). The Pradel model is only able to fit one recapture probability per sex and thus it was not possible to estimate separate recapture probabilities for the different attractants. Hence, the estimated recapture probabilities represent averages over the different attractants used in each study. To fit all four parameters, two equivalent formulations of the Pradel model (parameterized in terms of f , ϕ and p , and λ , ϕ and p , respectively) were fit.

Goodness-of-fit

The Pradel model assumes that different individuals in the marked population are statistically independent and that f , ϕ , λ and p are homogenous (i.e. do not vary among individuals). Violation of these assumptions or biologically unrealistic model structure can cause the model to fail to adequately fit the data (Burnham *et al.*, 1987; Lebreton *et al.*, 1992). The Cormack–Jolly–Seber mark–recapture model (Cormack, 1964; Jolly, 1965; Seber, 1965) is related to the Pradel model but is formulated in terms of parameters ϕ and p alone. Adequate goodness-of-fit of the Cormack–Jolly–Seber model (under the same assumptions of independence and homogeneity described above) implies proper fit for the Pradel model also, because the lack of fit of the Pradel model is a function of the recaptures portion of the likelihood, which is equal to the likelihood of the Cormack–Jolly–Seber model. Thus, in Program MARK, goodness-of-fit of the Pradel model is assessed by evaluating the goodness-of-fit of the proxy Cormack–Jolly–Seber model.

The record of captures and recaptures for each individual recorded in a mark–recapture dataset constitutes its encounter

Table 1. Mark–release–recapture datasets.

Site/Study	Position*	Dates	Holdridge life zone†	Season	Attractant	Flies marked	Flies recaptured	Publications
EJN‡								
1	10°19.399' N 85°8.447' W	23/01/1989; 19/03/1989	Tropical dry forest	Dry	Liver	♀ 1809; ♂ 190	♀ 1009; ♂ 18	Parker & Welch (1992); Matlock <i>et al.</i> (1996) Study 1§
2	10°20.093' N 85°8.344' W	01/09/1989; 30/10/1989	Tropical dry forest	Wet	Liver and sheep	♀ 2269; ♂ 165	♀ 646; ♂ 7	Parker <i>et al.</i> (1993); Matlock <i>et al.</i> (1996) Study 2§
3	10°20.105' N 85°8.296' W	23/01/1990; 23/03/1990	Tropical dry forest	Dry	Liver and sheep	♀ 1149; ♂ 136	♀ 483; ♂ 19	Parker <i>et al.</i> (1993); Matlock <i>et al.</i> (1996) Study 3§
4	10°19.180' N 85°7.929' W	18/04/1990; 11/01/1991	Tropical dry forest	Wet	Liver	♀ 3582; ♂ 289	♀ 656; ♂ 23	Matlock <i>et al.</i> (1996) Study 4§
Montezuma¶								
5	10°39.970' N 85°3.779' W	22/10/1991; 27/01/1992	Tropical premontane wet forest	Wet	Liver and SWL IV	♀ 1323; ♂ 298	♀ 268; ♂ 23	Matlock <i>et al.</i> (1996) Study 5§
6	10°39.936' N 85°3.765' W	27/01/1992; 03/04/1992	Tropical premontane wet forest	Dry	Liver and SWL IV	♀ 485; ♂ 205	♀ 70; ♂ 25	
7	10°40.413' N 85°4.006' W	06/04/1992; 11/12/1992	Tropical premontane wet forest	Wet	Liver	♀ 4380; ♂ 729	♀ 703; ♂ 39	Matlock <i>et al.</i> (1996) Study 6§
8	10°40.098' N 85°3.673' W	11/01/1993; 31/05/1993	Tropical premontane wet forest	Dry	Liver	♀ 2097; ♂ 467	♀ 441; ♂ 46	Matlock <i>et al.</i> (1996) Study 7§

*Mean latitude and longitude of observation stations.

†See text for references.

‡Enrique Jimenez Nuñez Experiment Station of the Costa Rican Ministry of Agriculture, 21 km south of Cañas, Guanacaste Province, Costa Rica.

§Study number in Matlock *et al.* (1996).

¶Hacienda Montezuma, 3 km southwest of Rio Naranjo, Guanacaste Province, Costa Rica.

history. This encounter history is typically represented as a binary string of 1s (for captures and recaptures) and 0s (for samples where the animal was not observed), where the number of digits in the string is equal to the total number of samples collected (Burnham *et al.*, 1987; Lebreton *et al.*, 1992). For example, the encounter history '010101' represents an animal captured for the first time in the second sample of a six-sample survey, recaptured in the fourth and sixth samples, but not observed in the odd-numbered samples. The maximum number of parameters, k , that can be fit with a mark–recapture dataset is equal to s , the number of unique encounter histories observed. Models for which $k = s$ are said to be saturated (full rank) (Burnham *et al.*, 1987; Lebreton *et al.*, 1992), whereas for $k < s$ (as is true for the models fit in this study), models are classified as unsaturated or reduced.

Lack of fit of unsaturated models is measured by the Deviance:

$$\text{Deviance} = 2\ln L_{\text{sat}}(\hat{\theta}_{\text{sat}}) - 2\ln L(\hat{\theta})$$

where $L_{\text{sat}}(\hat{\theta}_{\text{sat}})$ and $L(\hat{\theta})$ are the likelihoods of the saturated and unsaturated models, respectively, where both likelihoods are evaluated at the maximum likelihood estimates of their respective parameter vectors $\hat{\theta}_{\text{sat}}$ and $\hat{\theta}$ (Lebreton *et al.*, 1992). Provided the reduced model is structurally sound biologically, the Deviance is asymptotically distributed central χ^2 for large sample sizes, with $v = v_{\text{sat}} - k$ degrees of freedom (d.f.), where $v_{\text{sat}} = s - w$ is the d.f. associated with the saturated model, w is the number of samples in which at least one animal was caught and marked for the first time and k is the number of parameters fit in the reduced model. When the parameters are fit for more than one group (e.g. males and females), the log-likelihoods and d.f. are tallied independently for each group and summed.

The variance inflation factor, \hat{c} , is defined as:

$$\hat{c} = \frac{\text{Deviance}}{v}$$

If the assumptions of structural adequacy, statistical independence and homogeneity of recapture and survival rates are met, $\hat{c} = 1$, otherwise $\hat{c} > 1$. Thus, \hat{c} -values ≈ 1 imply satisfactory model fit, whereas $\hat{c} > 3$ implies a significant lack of fit between model and data (Lebreton *et al.*, 1992). We estimated \hat{c} using the median \hat{c} simulation procedure contained within Program MARK; \hat{c} -values from five repetitions of median \hat{c} procedure with 49 design points and three replicates at each design point were averaged and the standard error calculated as $\text{SE} = s_{\hat{c}}/\sqrt{5}$, where $s_{\hat{c}}$ is the mean standard deviation (SD) of the \hat{c} estimates for the five repetitions.

Parameter adjustment

If \hat{c} is > 1 , the variances of parameter estimates will be inflated by a factor \hat{c} . Hence, the SE of parameter estimates should be adjusted to $\text{SE} = \text{SE}(\hat{\theta})\sqrt{\hat{c}}$ (Lebreton, 1992). Thus, the SE of parameter estimates f , ϕ , λ and p were adjusted by multiplying by $\sqrt{\hat{c}}$, where \hat{c} is the average of the median \hat{c} -values generated by the median \hat{c} procedure.

Meta-analysis

To investigate whether the estimates f , ϕ and λ varied between sexes or were influenced by Holdridge life zone or the season in which the data were collected, the parameter estimates from the eight datasets were analysed with factorial, weighted analysis of variance, the weight for each observation being $1/\text{SE}^2$, where SE is the standard error of the parameter estimate calculated by MARK (Table 2, discussed in Results and Discussion). A simple additive model was fit, because insufficient d.f. were available to estimate all interaction terms. A second weighted ANOVA was conducted to determine whether recapture probabilities, p , varied with sex, season or type of attractant (liver, liver + sheep, liver + SWL IV).

Results and Discussion

Parameter estimates, SEs and 95% confidence intervals (CIs) are displayed in Table 2. Median \hat{c} measures of goodness-of-fit are displayed in Table 3. All median \hat{c} -values were ≈ 1 , suggesting that the Pradel model adequately fit the data. Parameter SEs were adjusted by the mean median \hat{c} estimates, $\bar{\hat{c}}$.

Meta-analysis

Holdridge life zone and sex had no significant effects on f , ϕ and λ . However, as the numbers of males released and recaptured were much smaller than those for females, statistical power for detecting differences between sexes was limited. The effect of season on ϕ was nearly significant ($F_{1,13} = 3.48$, $0.05 < P < 0.1$), with daily survivorship being 3% greater in the wet than the dry season, corresponding to extension of mean lifespan by approximately 1 day during the wet season. Recapture probability, p , varied with sex ($F_{1,13} = 18.17$, $P < 0.001$) and season ($F_{1,13} = 14.66$, $P < 0.005$) and the combination of the two variables explained 74% of the variation in p . Females were nearly six times as likely to be recaptured as males (Table 2) and flies were three times as likely to be recaptured in the dry than the wet season (weighted $p \pm \text{SE}$: dry 0.153 ± 0.036 ; wet 0.048 ± 0.013). Attractant had no significant impact on recapture probability ($F_{2,13} = 0.45$, $P > 0.05$). It is difficult to assess differences among the three attractants, however, because sheep and SWL IV were always used in combination with liver. Weighted mean parameter estimates (the weighting factor being $1/\text{SE}^2$ as in weighted ANOVA), SEs and 95% CIs are presented in Table 2. Sexes were combined for weighted mean parameter estimates of f , ϕ and λ ; separate weighted means are presented for males and females for p .

Comparison with published life history parameter estimates

Recruitment rate, survivorship and population growth are interrelated by the equation: $\lambda = \phi + f$ (Pradel, 1996). Hence, comparisons with published life history parameters are restricted to ϕ and λ . The Appendix gives estimates of the 10 parameters needed to estimate λ : ϕ_e , ϕ_l and ϕ_p , the probability of surviving the egg, larval and pupal phases, ϕ_a , the adult daily

Table 2. Pradel model parameter estimates.

Parameter	Study	Sex	Estimate	Standard error	95% lower confidence interval	95% upper confidence interval
ϕ	1	O ₃ +O	0.801	0.005	0.791	0.811
		O ₃	0.761	0.045	0.662	0.838
	2	O ₃ +O	0.822	0.006	0.809	0.834
		O ₃	0.772	0.094	0.544	0.906
	3	O ₃ +O	0.762	0.008	0.745	0.778
		O ₃	0.821	0.042	0.725	0.889
	4	O ₃ +O	0.801	0.006	0.789	0.813
		O ₃	0.759	0.042	0.667	0.832
	5	O ₃ +O	0.700	0.015	0.670	0.728
		O ₃	0.783	0.044	0.685	0.857
	6	O ₃ +O	0.700	0.028	0.643	0.752
		O ₃	0.709	0.045	0.613	0.790
	7	O ₃ +O	0.819	0.006	0.807	0.829
		O ₃	0.879	0.018	0.838	0.911
	8	O ₃ +O	0.749	0.010	0.730	0.767
		O ₃	0.766	0.031	0.701	0.821
	Weighted \bar{x}^*		0.798	0.008	0.780	0.815
f	1	O ₃ +O	0.166	0.005	0.156	0.176
		O ₃	0.201	0.045	0.127	0.304
	2	O ₃ +O	0.175	0.006	0.162	0.187
		O ₃	0.208	0.094	0.079	0.444
	3	O ₃ +O	0.213	0.008	0.197	0.230
		O ₃	0.120	0.041	0.060	0.227
	4	O ₃ +O	0.207	0.006	0.195	0.219
		O ₃	0.249	0.042	0.175	0.340
	5	O ₃ +O	0.284	0.015	0.257	0.314
		O ₃	0.197	0.044	0.125	0.297
	6	O ₃ +O	0.283	0.028	0.232	0.341
		O ₃	0.274	0.045	0.194	0.371
	7	O ₃ +O	0.187	0.006	0.176	0.198
		O ₃	0.126	0.018	0.094	0.167
	8	O ₃ +O	0.254	0.010	0.236	0.273
		O ₃	0.245	0.031	0.190	0.310
	Weighted \bar{x}^*		0.193	0.008	0.175	0.211
λ	1	O ₃ +O	0.967	0.002	0.964	0.970
		O ₃	0.962	0.005	0.951	0.971
	2	O ₃ +O	0.996	0.001	0.992	0.998
		O ₃	0.979	0.005	0.966	0.988
	3	O ₃ +O	0.975	0.002	0.971	0.979
		O ₃	0.942	0.007	0.926	0.954
	4	O ₃ +O	1.008	0.0003	1.008	1.009
		O ₃	1.008	0.001	1.006	1.010
	5	O ₃ +O	0.984	0.001	0.982	0.986
		O ₃	0.980	0.002	0.975	0.984
	6	O ₃ +O	0.984	0.002	0.978	0.988
		O ₃	0.983	0.004	0.974	0.989
	7	O ₃ +O	1.005	0.0002	1.005	1.006
		O ₃	1.005	0.0005	1.004	1.007
	8	O ₃ +O	1.003	0.001	1.002	1.004
		O ₃	1.011	0.001	1.008	1.013
	Weighted \bar{x}^*		1.005	0.002	1.001	1.008

Continued

Table 2. Continued.

Parameter	Study	Sex	Estimate	Standard error	95% lower confidence interval	95% upper confidence interval
p	1	♀	0.234	0.006	0.222	0.247
		♂	0.038	0.012	0.020	0.069
	2	♀	0.100	0.005	0.091	0.110
		♂	0.012	0.008	0.003	0.044
	3	♀	0.329	0.012	0.307	0.353
		♂	0.033	0.012	0.016	0.069
	4	♀	0.078	0.004	0.071	0.086
		♂	0.035	0.011	0.019	0.063
	5	♀	0.163	0.012	0.140	0.188
		♂	0.034	0.010	0.019	0.061
	6	♀	0.102	0.016	0.075	0.137
		♂	0.081	0.021	0.048	0.134
	7	♀	0.061	0.003	0.056	0.067
		♂	0.011	0.002	0.007	0.017
	8	♀	0.130	0.008	0.116	0.146
		♂	0.049	0.011	0.032	0.075
	Weighted \bar{x}	♀	0.099	0.023	0.045	0.153
		♂	0.017	0.005	0.005	0.028

*Sexes combined because there was no significant difference between ♀♀ and ♂♂.

survivorship, t_e , t_p , t_n and t_g , the durations of the egg, larval, pupal and nulliparous (preoviposition) phases and gonotrophic cycle, respectively, and m , the clutch size.

Published estimates of mean and median longevity from sources in the Appendix were converted to daily survivorship probabilities by assuming constant mortality. Under this assumption, longevity (age at the time of death), x , is exponentially distributed:

$$f(x) = \mu e^{-\mu x} \quad (1)$$

with mean $\bar{x} = \frac{1}{\mu}$ and median $x_{\frac{1}{2}} = \frac{\ln(2)}{\mu}$. Survivorship to age x is then given by $\exp\left(-\frac{x}{\bar{x}}\right)$ and $\exp\left(-\ln(2)\frac{x}{x_{\frac{1}{2}}}\right)$, and daily survivorships become $\exp\left(-\frac{1}{\bar{x}}\right)$ and $\exp\left(-\frac{\ln(2)}{x_{\frac{1}{2}}}\right)$, respectively. When survivorships, l_x , were reported for periods of $x > 1$ day, they were

converted to a 1-day timescale by taking $\phi_a = (l_x)^{\frac{1}{x}}$. No attempts were made to convert SEs or other variability measures to the daily timescale.

Survivorship

Using field data on the age structure of an NWS adult population, Thomas & Chen (1990) estimated $\phi_a = 0.813$, which was similar to the Pradel estimates in Table 2. Estimates of ϕ_a for cage (Davis & Camino, 1968) and laboratory studies (remaining references in the Appendix) all exceeded 0.9, being universally higher than the Pradel estimates (Table 2). Three (mutually compatible) explanations for the differences between the field and laboratory cage estimates are: (a) marking tags were lost and/or burdened marked flies, increasing mortality; (b) flies in the field were lost to emigration in addition to mortality, and (c) the adult flies experienced higher mortality in the field than in either the laboratory or cages (e.g. as a result of predation or other sources of mortality not experienced in confinement). Thomas & Chen's (1990) ϕ_a estimate was based on age structure determination by pteridine and involved no marking. Thus, loss of tags cannot explain the agreement between these authors' results and the mark-recapture estimates reported here. In a separate analysis, data for Studies 1–8 were fit to a diffusion model which simultaneously estimates the effects of mortality and emigration separately (R. B. Matlock & R. Skoda, in preparation). Mean (95% CIs) of survivorships for this analysis were: ♀♀ 0.947 (0.910–0.986); ♂♂ 0.886 (0.851–0.922). These estimates are higher than those in Table 2, suggesting that emigration may account for the difference between the Pradel

Table 3. Median \hat{c} goodness-of-fit statistics for Pradel model.

Study	Median \hat{c}	SEM
1	1.069	0.004
2	1.373	0.005
3	1.419	0.005
4	1.009	0.005
5	1.013	0.005
6	1.012	0.006
7	1.033	0.003
8	1.146	0.004

SEM, standard error of the mean.

and laboratory cage results. Predation or other sources of mortality may also have diminished survivorship. Thomas (1991) reported that screwworm adults in field cages were under constant threat from ants, especially while feeding on nectar.

Population growth rate

The λ value estimated by the Pradel model is the growth rate of the adult age class, which is not equal to the growth rate of the entire population unless the population is at stable age distribution. Once the age distribution is stationary, all age classes (and the population as a whole) grow at the same rate, λ . Insect populations with long growing seasons are more likely to be at stable age distribution (Taylor, 1979). Thus, stable age distribution is a reasonable assumption for NWS, which is active throughout the year in tropical climates and has no diapause period. Under stable age distribution, λ may also be calculated from Euler's equation:

$$\sum_{x=0}^{\infty} \lambda^{-x} l_x m_x = 1 \quad (2)$$

where l_x and m_x are the probability of survival to age x and the mean fecundity at age x , respectively. To estimate λ for NWS females from parameter values in the Appendix, we make the following assumptions: (a) that daily adult survivorship takes the constant value ϕ_a throughout adulthood, including the preoviposition period; (b) that fecundity $m_x = ihm/2$, where i is the probability the female has mated and is inseminated, h is the probability she finds a suitable host and m is the constant, mean clutch size ($m/2$ being the number of female offspring per oviposition), and (c) that females oviposit at a fixed time interval following the initial oviposition, t_g being the length of the gonotrophic cycle. Given these assumptions, equation (2) becomes:

$$\sum_{x=0}^{\infty} \lambda^{-(t_e + t_l + t_p + t_n + t_g x)} \phi_e \phi_l \phi_p \phi_a^{t_n} \phi_a^{t_g x} i h \frac{m}{2} = 1 \quad (3)$$

Equation (3) sums to:

$$\frac{\phi_e \phi_l \phi_p \phi_a^{t_n} i h \frac{m}{2} \lambda^{t_g - (t_e + t_l + t_p + t_n)}}{\lambda^{t_g} - \phi_a^{t_g}} = 1, \quad (4)$$

λ being given by the single real root of (4). To calculate numerical estimates of λ from equation (4) and parameter values in the Appendix, we make the following assumptions with regard to parameter ranges:

- 1 Egg development time, t_e , is 1 day (Laake *et al.*, 1936; Smith, 1960; Baumhover, 1966; Davis & Camino, 1968) and survivorship through the egg phase is $0.9 \leq \phi_e \leq 1.0$ (Laake *et al.*, 1936; Baumhover, 1966; Davis & Camino, 1968; Taylor, 1988; Taylor & Mangan, 1987; Friese, 1992).
- 2 Based on estimates for larvae reared on wounds in sheep (Laake *et al.*, 1936; Davis & Camino, 1968; Rubink, 1987; Thomas & Pruett, 1992), the larval period, t_l is 5–7 days and survivorship through the larval phase is $0.5 \leq \phi_l \leq 0.9$.
- 3 Pupal development time and survivorship are strongly temperature-dependent and estimates in the Appendix were

highly variable. Assumed ranges for prepupal (crawl-off) + pupal development time and survivorship are: 6 days $\leq t_p \leq 10$ days and $0.2 \leq \phi_p \leq 0.99$.

- 4 Adult daily survivorship ranges from: $0.8 \leq \phi_a \leq 0.98$ (range of estimates in the Appendix).
- 5 The proportion of females mated in field studies is generally high (Guillot *et al.*, 1977a, 1977b; Parker & Welch, 1991a; Parker *et al.*, 1993). Parker & Welch (1991a) reported that it was 100% for gravid females. Thus, we assume that $i = 1$ for females that survive through the nulliparous phase.
- 6 The length of the preoviposition (nulliparous) period, t_n , is 4–7 days, commensurate with tropical temperatures (Krafsur *et al.*, 1979; Thomas & Chen, 1990; Thomas, 1993).
- 7 The length of the gonotrophic cycle, t_g is 3 days, consistent with estimates in tropical forest habitats (Thomas & Mangan, 1989; Parker & Welch, 1991b; Parker *et al.*, 1993).
- 8 The probability of host location, h , cannot be estimated from current published literature. Therefore, we assume $h = 1$ (i.e. that hosts are always found).
- 9 Mean clutch size, $m = 200$, based on Thomas & Mangan's (1989) estimate for egg masses oviposited on wounds in tropical forest habitat in Mexico and Belize, similar to the habitats in Studies 1–8.

Estimates for λ from Table 2 ranged from 0.942 to 1.011, including both growing and declining populations, the weighted mean estimate being $\lambda = 1.005 \pm 0.002$. Under density-independent growth conditions such as those likely to prevail during outbreaks in screwworm-free territory, this would correspond to a doubling time of $t_2 = \ln(2)/\ln(\lambda) = 139$ days. By contrast, the estimate of λ from (4) for the least favourable parameter values for population growth specified in the assumed ranges 1–9 was 1.05, implying a population doubling time of 14 days. This was substantially greater than even the largest 95% CI for the Pradel model estimates in Table 2, 1.013 (σ^2 , Study 8), with a doubling time of 54 days. Parameter values typical of the screwworm production facility in Mexico are: $\phi_e = 0.9$ (Taylor, 1988; Friese, 1992; Taylor & Mangan, 1987), $t_e \leq 1$ (all references in the Appendix), $\phi_l = 0.9$ (Taylor & Mangan, 1987), $t_l = 6$ days (Taylor & Mangan, 1987; Taylor *et al.*, 1991), $\phi_p = 0.95$ (Taylor & Mangan, 1987; Taylor, 1988), $t_p = 9$ days (Thomas, 1989), $\phi_a = 0.95$ (Peterson *et al.*, 1983, 1987), $t_n = 6$ days (Thomas, 1993), $t_g = 3$ days (Thomas & Mangan, 1989; Parker & Welch, 1991b; Parker *et al.*, 1993) and $m = 250$ (Thomas, 1993). For these values of the parameters $\lambda = 1.25$, corresponding to a potential doubling time of 3 days under optimal conditions.

Assuming no net movement of the populations in Studies 1–8, errors in ϕ and f resulting from emigration and immigration should tend to cancel one another out, affecting the Pradel model estimate of $\lambda = \phi + f$ less than that of ϕ . Hence, unlike adult survivorship, emigration seems less likely to explain the differences between Pradel and equation (4) estimates of λ . Many of the laboratory estimates of survivorship in the Appendix were calculated for near optimal conditions and probably overestimate rates in the field. Thomas (1989) reported, for

example, that larvae that pupated in soil exposed to direct sunlight experienced 77% mortality. Development times are also typically shorter under constant temperature than in natural fluctuating thermal environments. Both could have contributed to the disagreement between the Pradel and equation (4) estimates. The least justifiable of assumptions 1–9 is that host location is certain. At stable age distribution, the proportion of the adult population that is of reproductive age, c_r , is given by:

$$c_r = \frac{\phi_e \phi_p \sum_{x=n}^{\infty} \lambda^{-t_e - t_p - x} \phi_a^x}{\phi_e \phi_p \sum_{x=0}^{\infty} \lambda^{-t_e - t_p - x} \phi_a^x} = \left(\frac{\phi_a}{\lambda} \right)^n$$

If the probability of finding a host, $h \approx 1$, then most females of reproductive age should be parous. In this case, c_r should be approximately equal to the proportion of parous females in the population. Taking $\lambda = 1.005$ (Table 2) and $0.8 < \phi_a < 0.9$ (Table 2, and Matlock and Skoda, in preparation), then $0.25 < c_r < 0.52$. Parker & Welch (1991a, 1991c, 1992) and Parker *et al.* (1993) reported parity fractions at Enrique Jimenez Nuñez Experiment Station, the site of Studies 1–4, in the range of 31–50%, which is consistent with this estimate. Female screwworm reabsorb eggs when they are unable to oviposit (Adams & Reinecke, 1979). Parker & Welch (1991a) reported that 2.9–6.8% of females contained eggs undergoing reabsorption, suggesting that the number of females that failed to find hosts was small. Thus, other life history traits, such as pupal survival, may be more likely to account for differences between Pradel estimates and equation (4).

Doubling times for λ estimates in Table 2 ranged from 54 to 139 days, whereas the maximum doubling time calculated from the life history parameters in the Appendix was 14 days. Thus, it seems very plausible that screwworm outbreak populations could double in 1–2 months or faster. Given the difficulty of detecting sparse outbreak populations, the presence of undetectable phases in the life-cycle (e.g. pupae), and the likely inexperience with screwworm in countries where NWS is introduced (e.g. Libya; Krafus & Lindquist, [1996]), screwworm populations could easily double several times before discovery, underscoring the need for effective quarantine measures to protect livestock industries worldwide from the catastrophic costs of screwworm introduction.

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Conflicts of interest

All authors declare no conflicts of interest.

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Appendix. Screwworm, *Cochliomyia hominivorax*, life history parameters.

Parameter	Source	Value	Notes
Proportion eclosing (ϕ_e)	Crystal (1967a)	0.873 ¹ , 0.86 ² , 0.887 ³ , 0.858 ⁴ , 0.851 ⁵ , 0.82 ⁶	¹ Fig. 3; ² Fig. 4; ³ Fig. 5; ⁴ Fig. 6; ⁵ Fig. 7; ⁶ p 447
	Devaney & Garcia (1975) Table 2	0.886 ¹ , 0.903 ² , 0.922 ³ , 0.919 ⁴ , 0.864 ⁵ , 0.863 ⁶ , 0.936 ⁷	Strain: ¹ OMS; ² NMS1; ³ NMS2; ⁴ NMS; ⁵ PRN; ⁶ CTX; ⁷ RF; 27 ± 2° C, 46–82% RH
	Friese (1992) Table 2	0.923	
	McInnis <i>et al.</i> (1983) Table 3	0.920 ¹ , 0.829 ²	^{1,2} Means for two strains
	Taylor (1988) Table 1	Mean ± SD: 0.896 ± 0.0221 ¹ , 0.913 ± 0.0155 ² , 0.832 ± 0.0577 ³ , 0.885 ± 0.0283 ⁴	Diet: ¹ Water lock; ^{2–4} Carageenan 25%, 37%, 50%
Egg development time (t_e)	Taylor & Mangan (1987) Table 1	Mean ± SD: 0.873 ± 0.0652 ¹ , 0.853 ± 0.0538 ²	Diet: ¹ Meat, ² Gel
	Baumhover (1966) p 242	16h	
	Davis & Camino (1968) Table 1	8–12h	For temperatures, see pupal development time
	Laake <i>et al.</i> (1936) p 4	11–21.5h ¹ , 9.2h ¹ , 13.9h ³	¹ On wounds; ^{2,3} 100% RH, 37.2° C and 28.9° C
	Parman (1945) p 73	8–24h	
Larval survivorship (ϕ_l)	Smith (1960) p 1112	12–14h	
	Thomas & Pruett (1992) Table 1	0.630 ± 0.142 ¹ , 0.585 ± 0.131 ² , 0.618 ± 0.110 ³ , 0.559 ± 0.028 ⁴	In wounds on sheep. Mean ± SD of four replicates each of four treatments: 25 ¹ , 50 ² , 100 ³ and 200 ⁴ larvae per host. Survival measured after 4 days of infestation
	Laake & Smith (1939) p 340	0.820 ¹ , 0.797 ² , 0.806 ³ , 0.902 ⁴	In wounds in cavies (presumably guinea pigs). ¹ Initial infestation; ² first re-infestation; ³ second re-infestation; ⁴ third re-infestation
	Milward de Azevedo <i>et al.</i> (1992) Table 4	0.520	38° C
	Rubink (1987) p 602	0.050–0.950 ¹ , 0.035–0.985 ²	Larvae reared in wounds in sheep. ¹ 0–19 larvae per host; ² 23–193 larvae per host
Taylor & Mangan (1987) Tables 1 and 4		0.632 ¹ , 0.880 ²	Diet: ¹ Meat, ² Gel. Calculated as: $I_L = \frac{n}{1,350 \times I_E \times 9}$ where n is number of larvae in Table 4, 1350 is number of larvae in 50mg eggs, I_E is the proportion of eggs (see above) and 9 is number of lines examined

Continued

Appendix. Continued.

Parameter	Source	Value	Notes
Larval development time (t_l)	Baumhover <i>et al.</i> (1966) p 545	4–6 days	In wounds in sheep. See notes for adult survivorship for approximate minimum ambient temperatures
	Davis & Camino (1968) Table 1	7 days	Horsemeat diet; $27 \pm 2^\circ\text{C}$
	Hightower <i>et al.</i> (1971) p 1475	3.75–5.04 days (90.1–120.9 h)	¹ Sheep; ² cattle
	Laake <i>et al.</i> (1936) p 24	4.3–7.3 days (103.8–174.5 h) ¹ , 3.4–10.0 days (82–239 h) ²	
	Milward de Azevedo <i>et al.</i> (1992) Table 2	6.35 \pm 0.63	38°C
	Rubink (1987) p 602	4.97 \pm 0.25 days ¹ , 5.70 \pm 0.57 days ²	Mean \pm SD of median crawl-off time for larvae reared in wounds in sheep. ¹ 0–19 larvae per host; ² 23–193 larvae per host
	Taylor & Mangan (1987) Table 3	6.0 \pm 1.1 (143.2 h) ¹ , 6.5 \pm 0.9 (156.5 h) ² , 6.5 \pm 0.9 (154.8 h) ³	Reared on artificial diets: ¹ Meat; ² Gel G-400; ³ Gel G-100. 35–39°C, 70–75% RH
	Taylor <i>et al.</i> (1991) p 5	5.18 \pm days (124.4 h) ¹ , 5.27 days (126.4 h) ²	Reared on artificial diets: ¹ hydroponic; ² water lock; 35–39°C, 70–75% RH
	Baumhover (1963) p 475	0.955 ¹ , 0.960 ² , 0.937 ³	¹ 32.2°C, 85% RH; ² 32.2°C with 2-inch sand cover; ³ 26.7°C, 85% RH Prepupal + pupal period
	Cardoso <i>et al.</i> (1992) Table 2	0.588 ¹ , 0.55 ² , 0.638 ³ , 0.813 ⁴ , 0.775 ⁵ , 0.325 ⁶ , 0.613 ⁷	Emergence rates for seven pupation substrates. Prepupal + pupal period
Pupal survivorship (ϕ_p)	Deonier (1945) p 93, Table 3	0.360 ¹ , 0.460 ² , 0.220 ³ , 0.880 ⁴ , 0.380 ⁵ , 0.660 ⁶ , 0.200 ⁷ , 0.220 ⁸ , 0.700 ⁹	^{1–3} Range soil, 9.5°C, 11.8°C, 12.8°C, ^{4–6} cultivated soil, 13.3°C, 11.9°C, 12.4°C; ⁷ manure, 10.2°C, 11.8°C, 12.4°C. Prepupal + pupal period
	Flitters & Benschoter (1971) p 66, Table 1	0.17 ¹ , 0.07 ² , 0.00 ³	¹ p 66, $\bar{T} = 12.2^\circ\text{C}$; ² p 66, $\bar{T} = 10.0^\circ\text{C}$; ³ Table 1. $\bar{T} = 6.5^\circ\text{C}$. Pupal period only
	Friese (1992) Table 1	0.919	27°C, pupal period only
	Hightower <i>et al.</i> (1971) Table 4	0.934	^{1–8} Means for eight selected strains, pupal period only
	McGinnis <i>et al.</i> (1983) Table 3	Mean \pm SD: 0.923 \pm 0.0061 ¹ , 0.935 \pm 0.0112 ² , 0.918 \pm 0.0044 ³ , 0.895 \pm 0.0156 ⁴ , 0.827 \pm 0.0393 ⁵ , 0.797 \pm 0.0720 ⁶ , 0.800 \pm 0.0682 ⁷ , 0.780 \pm 0.0597 ⁸	
	Milward de Azevedo <i>et al.</i> (1992) Table 4	0.889	25°C, 60% RH. Pupal period only
	Taylor (1988) Table 1	0.988 ¹ , 0.960 ² , 0.959 ³ , 0.949 ⁴	Diet: ¹ water lock; ² -Carageenan 25%, 37%, 50%. Pupation in sawdust
	Taylor & Mangan (1987) Table 1	0.909 ¹ , 0.942 ²	Diet: ¹ Meat; ² Gel
	Taylor <i>et al.</i> (1991) Table 1	0.930 ¹ , 0.864 ² , 0.961 ³ , 0.956 ⁴	¹ Hydroponic (experimental); ² hydroponic (production); ³ water lock 2g; ⁴ water lock 3g. 30.0°C, 60% RH, pupal period only
	Thomas (1989) Table 2	0.915 ¹ , 0.229 ² , 0.597 ³ , 0.753 ⁴	¹ Indoors (control); ² exposed, $\bar{T}_{\min} = 20.2^\circ\text{C}$, $\bar{T}_{\max} = 33.7^\circ\text{C}$; ³ semi-shade; ⁴ shade, $\bar{T}_{\min} = 22.2^\circ\text{C}$, $\bar{T}_{\max} = 32.5^\circ\text{C}$. Pupal period only

Continued

Appendix. Continued.

Parameter	Source	Value	Notes
Pupal development time (t_p)	Cardoso <i>et al.</i> (1992) Table 2	Mean (95% CI): 9.29 (9.03–9.55) days, 9.26 (8.97–9.55) days, 9.19 (8.99–9.39) days, 9.65 (9.15–10.15) days, 9.25 (8.9–9.6) days, 10.14 (9.74–10.54) days, 9.38 (8.79–9.97) days	Pupation time for seven pupation substrates. 27.0 °C, 65 ± 10% RH
	Davis & Camino (1968) Table 1, Fig. 1	12 days ¹ , 12 days ² , 12 days ³ , 9 days ⁴ , 9 days ⁵	^{1–3} See corresponding notes for adult survivorship for approx. minimum ambient temperatures; ^{4,5} greenhouse 5–8 °C warmer than ambient temperatures ^{1–3}
	Deonier (1945) p 93, Table 3	34 days ¹ , 50 days ² , 47.5 days ³ , 39 days ⁴ , 59.5 days ⁵ , 44 days ⁶ , 36.5 days ⁷ , 47.5 days ⁸ , 41.5 days ⁹	See notes for pupal survivorship
	Laake <i>et al.</i> (1936) p 19	5.93 days (142.2 h) ¹ , 31.7 days (760.4 h) ²	¹ 34.4 °C; ² 15.0 °C
	Milward de Azevedo <i>et al.</i> (1992) Table 4	8–10 days	25 °C
	Parman (1945) p 70	Approximate development times: 10 days ¹ , 15 days ² , 30 days ³	¹ 23.9 °C; ² 21.1 °C; ³ 15.5 °C
	Smith (1960) p 1111	6.50–9.34 days	26.7 °C, 50–60% RH, pupal period only
	Thomas (1989) p 323	8–9 days	See notes for pupal survivorship
Adult survivorship (ϕ_a)	Adams (1979) Fig. 2	0.965 ± 0.000135	Weighted mean of daily survivorship between 12.8 °C and 37.8 °C (survivorship was nearly constant over this temperature range), weighted by number of flies assayed
	Baumhover (1965) p 545	♂♂ 0.950, ♀♀ 0.980	74% and 46% survivorship @ 15 days, 26.7 °C for ♀♀ and ♂♂ caged alone, corresponding to ♀♀
	Crystal (1967b) Table 1	0.957 ¹ , 0.966 ² , 0.976 ³ , 0.957 ⁴ , 0.975 ⁵ , 0.980 ⁶	$\phi = 0.74^{15} = 0.980$ and $\phi = 0.46^{15} = 0.950$ ^{1–3} ♂♂ mixed sexes, unisexual, individual, respectively; ^{4–6} ♀ mixed sexes, unisexual, individual, respectively.
	Davis & Camino (1968) Fig. 1A–C	0.965 ± 0.011 ¹ , 0.917 ± 0.0163 ² , 0.905 ± 0.0225 ³	27 °C, 60% RH; calculated from mean longevity (see text) ϕ estimated by fitting model: $l(t) = \phi^t$ with non-linear regression, where $l(t)$ is survivorship to time t . ¹ Fig. 1A.
	Devaney & Garcia (1975) Table 1	♂♂: 0.900 ¹ , 0.914 ² , 0.913 ³ , 0.930 ⁴ , 0.934 ⁵ , 0.943 ⁶ , 0.938 ⁷ ; ♀♀: 0.904 ¹ , 0.908 ² , 0.911 ³ , 0.924 ⁴ , 0.940 ⁵ , 0.930 ⁶ , 0.944 ⁷	$\bar{T}_{min} = 14$ °C. Approximate $F_{1,6} = 57.83$; $P < 0.0005$. ² Fig. 1B. $\bar{T}_{min} = 13.9$ °C. Approximate $F_{1,6} = 87.56$; $P < 0.0001$. ³ Fig. 1C. $\bar{T}_{min} = 16.9$ °C. Approximate $F_{1,6} = 63.74$; $P < 0.0005$ Strain: ¹ OMS, ² NMS1, ³ NMS2, ⁴ NMS, ⁵ PRN, ⁶ CTX, ⁷ RF. 26.5 ± 1.5 °C, 20–68% RH; calculated from mean longevity (see text)

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Appendix. Continued.

Parameter	Source	Value	Notes
Length of preoviposition period (t_p)	Hightower & Garcia (1972) Table 1 Controls	$\delta\delta$: 0.944, 0.944, 0.939; $\sigma\sigma$: 0.953, 0.958, 0.956	33 °C; calculated from mean longevity (see text)
	Milward de Azevedo <i>et al.</i> (1992) Figs 7–10	0.911 ¹ , 0.934 ² , 0.924 ³ , 0.945 ⁴	ϕ estimated by fitting model: $l(t)=\phi^t$ with non-linear regression, where $l(t)$ is survivorship to time t . ¹ Fig. 7: $\delta\delta$, 27 °C, 60% RH; ² Fig. 8: $\sigma\sigma$, 27 °C, 60% RH; ³ Fig. 9: $\delta\delta$, 25 °C, 60% RH; ⁴ Fig. 10: $\sigma\sigma$, 25 °C, 60% RH
	Peterson <i>et al.</i> (1983) Table 1	0.973 ¹ , 0.944 ²	¹ Fertile $\delta\delta$; ² sterile $\delta\delta$. \bar{T}_{\min} = 24.4 °C. \bar{T}_{\max} = 27.4 °C. 54.6–74.1% RH; calculated from median longevity (see text)
	Peterson <i>et al.</i> (1987) p 132	0.965 ¹ , 0.964 ²	¹ Fertile $\sigma\sigma$; ² fertile $\delta\delta$. 27 °C, 65% RH, honey and water; calculated from median longevity (see text)
	Spates & Hightower (1967) Figs 1 and 2	$\delta\delta$: 0.931 ¹ , 0.944 ² , 0.947 ³ , 0.951 ⁴ , 0.957 ⁵ , 0.962 ⁶ ; $\sigma\sigma$: 0.968 ¹ , 0.968 ² , 0.974 ³ , 0.976 ⁴ , 0.978 ⁵ , 0.979 ⁶	Six strains: ¹ BR, ² KC, ³ PR, ⁴ MC, ⁵ SC, ⁶ FL. BR is significantly different from the rest
	Spates & Hightower (1970) p 1382	0.961 ¹ , 0.976 ² , 0.962 ³ , 0.976 ⁴	$\delta\delta$: ¹ Lab strain, ² wild-type; $\sigma\sigma$: ³ lab strain, ⁴ wild-type. 27 °C, 60% RH; calculated from median longevity assuming constant survivorship (see text)
	Thomas & Chen (1990) p 1426	0.813	Field estimate based on age structure. \bar{T}_{\min} = 22 °C (range 20–24 °C). \bar{T}_{\max} = 33 °C (range 32–37 °C)
	Adams (1979) Table 2	37.9 days (909 h) ¹ , 3.4 days (81 h) ²	¹ 15.6 °C; ² 32.2 °C
	Adams & Reinecke (1979) Table 4 (Stage 10)	6.33 days (152 h) ¹ , 3.33 days (80 h) ²	¹ 24 °C; ² 30 °C
	Hammack (1991) p 189	5 days	25 °C, 50% RH
Length of gonotrophic cycle (t_g)	Hightower <i>et al.</i> (1972) Table 1	Mean \pm SD: 4.8 \pm 1.2 days, mode 4 days ¹ ; mean \pm SD: 11.1 \pm 1.1 days, mode 8 days ²	¹ Lab strain; ² wild-type. 24–26 °C, 35–60% RH
	Krafsur <i>et al.</i> (1979) p 477	17 days ¹ , 6 days ^{2,3} , 8 days ⁴ , 4 days ⁵	Strain 001: ¹ 15 °C, ² 25 °C, ³ 30 °C; ⁴ strain CTX, 25 °C; ⁵ Florida strain, 25 °C
	Laake <i>et al.</i> (1936) p 20	5–10 days	¹ \bar{T}_{\min} = 22 °C (range 20–24 °C); ² \bar{T}_{\max} = 33 °C (range 32–37 °C)
	Thomas & Chen (1990) p 1425	4 days ¹ , 7 days ²	¹ 30 °C; ² 22 °C
	Thomas (1993) Table 1	4–6 days ¹ , 8–10 days ²	¹ Between first and second oviposition, wild-type; ² between first and second oviposition, lab strain; ³ between succeeding ovipositions, both strains; 24–26 °C, 35–60% RH; 36–38 °C oviposition substrate
	Hightower <i>et al.</i> (1972) p 229	5.4 days ¹ , 3.2 days ² , 3.0 days ³	¹ Between first and second oviposition, wild-type; ² between first and second oviposition, lab strain; ³ between succeeding ovipositions, both strains; 24–26 °C, 35–60% RH; 36–38 °C oviposition substrate
	Parker & Welch (1991b) p 1470	Mean 3.3 days (range 2–4 days)	$\sigma\sigma$ visiting wounded sheep. Wet season: 25.4 °C, 78% RH; dry season: 27.9 °C, 60.4% RH
	Parker <i>et al.</i> (1993) Fig. 10B	Mode 3 days (range 1–7 days)	

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Appendix. Continued.

Parameter	Source	Value	Notes
Clutch size (<i>m</i>)	Thomas & Mangan (1989) Fig. 2	3 days	27 °C, 60% RH; 37 °C oviposition substrate Strain: ¹ OMS, ² NMS1, ³ NMS2, ⁴ NMS, ⁵ PRN, ⁶ CTX, ⁷ RF. 27 ± 2 °C, 46–82% RH. Oviposition substrate 35 °C
	Crystal & Meyners (1965) p 215	200–250	
	Devaney & Garcia (1975) Table 2	290 ¹ , 236 ² , 255 ³ , 260 ⁴ , 214 ⁵ , 241 ⁶ , 266 ⁷	
	Laake <i>et al.</i> (1936) p 5	10–393	¹ Laboratory strain; ² wild-type ¹ p 1468, wound-reared blue-curly mutant laboratory strain; ^{2,3} p 1469, 5- and 6-day-old wound-reared Belize strain, Table 2, 22 °C; ⁴ Guatemala strain; ⁵ Belize strain, Table 3, 30 °C; ⁶ Guatemala strain; ⁷ Belize strain On wounds on sheep
	Milward de Azevedo <i>et al.</i> (1992) Table 4	227.44 ± 10.85	
	Spates & Hightower (1970) Fig. 5	307 ± 1.59 ¹ , 331 ± 1.88 ²	
	Thomas (1993)	285.2 ± 17.0 ¹ , 283.3 ² , 277.7 ³ , 225.8 ⁴ , 223.3 ⁵ , 149.3 ⁶ , 203.2 ⁷	
	Thomas & Mangan (1989) Table 3	199.7 ± 6.0	

Numerical footnotes in the Value column apply only to the Notes to the immediate right within the same row. All parameters are for fertile screwworm flies unless otherwise stated. Daily survivorships are reported for adults. Survivorships and development time for the larval and pupal phases are for the complete life stages. When stipulated, survivorship for the prepupal (crawl-off) period is combined with the pupal stage; otherwise the prepupal (crawl-off) survivorship is not reported. Variability estimates associated with means are standard errors unless otherwise stipulated.